Estimation of Individual Growth Rates and Number of Age Classes in Sub-adult, Benthic Populations of Three Species of Sea Turtles in Southeastern U.S. Waters

Final Report to the National Marine Fisheries Service
Southeast Regional Office, Federal Grants Program
9721 Executive Center Drive, N., St. Petersburg, FL 33702.
MARFIN Project Number NA57FF0063. 48 pp.

December 1996
Revised April 1997

Karen A. Bjorndal and Alan B. Bolten

Archie Carr Center for Sea Turtle Research
Department of Zoology
University of Florida
Gainesville, Florida 32611

Based on sea turtle stranding data provided by State and Federal Coordinators (listed in alphabetical order):

Gary Hopkins, Bruce Koike, Charles Maley, Barbara Schroeder, Donna Shaver, Robert Shipp, and Wendy Teas

EXECUTIVE SUMMARY

1. The objectives of this project were to use length-frequency analyses to estimate individual growth rates and number of age classes in sub-adult benthic populations for loggerheads (*Caretta caretta*), Kemp's ridleys (*Lepidochelys kempi*), and green turtles (*Chelonia mydas*) in the waters of the southeastern United States. Originally, an objective was to identify ages at sexual maturity for these populations, but recent advances in our understanding of sea turtle population structure, attainment of sexual maturity, and growth make it clear that estimates generated from the intended methodology are quite unreliable (see #4 and #7 below).

2. Four length-frequency analysis programs were tested in this study: ELEFAN I, Shepherd's length composition analysis, projection matrix, and MULTIFAN. The first three programs failed to identify a best fit and thus failed to generate von Bertalanffy growth parameters. Therefore, we used only MULTIFAN for the evaluations presented in this report.

3. The MULTIFAN software used in this study was version 32(f) modified to include 30 age classes by Fournier (October 1996, pers. comm.). This software is produced by Otter Research Ltd., Nanaimo, B.C., Canada (Otter Research Ltd., 1992). Each analysis consisted of three runs: initial analysis, analysis in which standard deviations of age-class modes were allowed to vary, and analysis in which K was allowed to vary.

4. MULTIFAN uses the von Bertalanffy growth model. We did not extrapolate beyond the size range included in the analyses to estimate the age at sexual maturity because the appropriate size to use as size at sexual maturity is not known and we do not

know if the von Bertalanffy growth model is appropriate for these life stages. Studies in Australia (Chaloupka and Limpus, 1997; Limpus and Chaloupka, in press) and in the Atlantic (Chaloupka and Zug, in review; Bjorndal, Bolten and Chaloupka, in preparation) indicate that the von Bertalanffy model is not appropriate for some populations of sea turtles.

5. Length-frequency analyses were conducted on the size distribution data for stranded turtles compiled at the NOAA/NMFS Southeast Fisheries Science Center, Miami, from the Sea Turtle Stranding and Salvage Network for 1980 through 1995 for Georgia, Alabama, Mississippi, Louisiana and Texas. Data for 1988 through 1995 for Florida was received from the Florida Department of Environmental Protection. All turtles known to have been head-started were excluded from the analyses.
6. Limitations of length-frequency analyses with the sea turtle stranding database are discussed. Small monthly sample sizes required that we combine months from different years, which has confounded the length-frequency results. This was not the case with the Bahamian green turtle samples on which MULTIFAN was tested successfully where large, discrete sample sizes were available.
7. Any factor that obscures age class (or modal) structure makes length-frequency analysis more difficult. Such factors include long spawning season, variation in individual growth rates that result in variation in length-at-age, cessation or near cessation of growth in old age classes, and high rates of exploitation. If older age classes cannot be distinguished, K will be overestimated and the number of age classes will be underestimated (Terceiro et al., 1992). Because sea turtles essentially stop growing at sexual maturity and because they attain sexual maturity at a range of

sizes, the modes above the minimum size at sexual maturity are obscured and cannot be distinguished in length-frequency analyses. If length-frequency data sets are drawn from a wide geographic region, variation in growth rates over that region may result in obscured modal structure. Also, populations with very high exploitation may have reduced modal structure at the largest sizes.

8. The loggerhead size range for length-frequency analyses was limited to the size range over which age class modes could potentially be distinguished--the sub-adult, benthic lifestage: 46-87 cm CCL. Loggerhead stranding data were divided into 10 subsets (geographic and temporal). We ran a series of 27 length-frequency analyses using different combinations of database subsamples, initial parameter estimates, and designated month of recruitment.

9. MULTIFAN generated an estimate of 20 years as the time required for loggerheads along the Atlantic coast of Florida and in the Gulf of Mexico to grow from 46 to 87 cm CCL.

10. The Kemp's ridley size range for length-frequency analyses was limited to the size range over which modes could potentially be distinguished--the sub-adult, benthic lifestage: 20-61 cm CCL. The Kemp's ridley stranding data were divided into 3 data sets (geographic). We ran a series of 10 analyses with MULTIFAN software using different combinations of database subsamples, initial parameter estimates, and designated month of recruitment.

11. The best fit for Kemp's ridleys generated by MULTIFAN was for the Gulf of Mexico sample. That fit estimated that 15 years are required for a Kemp's ridley to grow from 20 cm to 61 cm CCL.

12. The size range for length-frequency analyses for green turtles was limited to the size range over which modes could potentially be distinguished--from 25 to 70 cm CCL. The only sample used in length-frequency analyses for green turtles was the turtles that stranded along the Atlantic coast of Florida from 1988 through 1995. The sample sizes in other regions were too small for length-frequency analysis. We ran a series of five analyses with MULTIFAN software using different combinations of database subsamples, initial parameter estimates, and designated month of recruitment.

13. MULTIFAN generated an estimate of 13 years as the time required for a green turtle to grow from 25 to 70 cm CCL. This result compared favorably to the 11-year estimate generated by MULTIFAN for green turtles in the warmer waters of the southern Bahamas (Bjorndal et al. 1995).

OBJECTIVES

The objectives of this project were to estimate individual growth rates and number of age classes in sub-adult benthic populations for three species of sea turtles in waters of the southeastern United States using length-frequency analyses. Originally, an objective was to identify ages at sexual maturity for these populations, but recent advances in our understanding of sea turtle population structure, attainment of sexual maturity, and growth make it clear that estimates generated from the intended methodology are quite unreliable. Length-frequency analyses were conducted on the size distribution data compiled at the NOAA/NMFS Southeast Fisheries Science Center Miami Laboratory and at the Florida Department of Environmental Protection from the Sea Turtle Stranding and Salvage Network for loggerheads, *Caretta caretta*; Kemp's ridleys, *Lepidochelys kempi*; and green turtles, *Chelonia mydas*.

INTRODUCTION

Individual growth rate in a population is a critical demographic parameter for understanding the life history of a species and for developing management plans for wild populations. Although growth studies based on mark and recapture of individual animals yield direct measures of growth rates, there are disadvantages to this approach. Mark and recapture studies can be very long term, labor-intensive efforts that require considerable investments of time and funds. The animal may be affected by the mark or tag, so that the measured growth rate is biased. Some species, or some lifestages of certain species, are not good subjects for mark and recapture studies because appropriate marking technology is not available or because the probability of recapture of a marked individual is very low. Bias in measurements taken by different observers may introduce an important source of variation.

In addition to the above general reservations, sea turtles have a number of characteristics that make them relatively poor candidates for mark and recapture growth studies. Sea turtles are slow growing, so mark and recapture studies are of necessity long term. The probability of recapture of marked individuals is low in many populations because of the characteristics of the lifestage (e.g., post-hatchlings in a pelagic habitat), high natural mortality in young lifestages, and high human-induced mortality in juvenile and adult lifestages. Growth models based on mark and recapture studies have been generated for several populations of a few species of sea turtles (e.g., Balazs, 1982; Bjorndal and Bolten, 1988; Boulon and Frazer, 1990; Frazer and Ehrhart, 1985; Limpus, 1992; Schmid, 1995; Chaloupka and Limpus, 1997; Limpus and Chaloupka, in press). However, to generate the regional management plans required to ensure the survival of these species, estimates of growth rates are needed for all species of sea turtles and for more populations within each species.

Length-frequency analysis has been used for many years to estimate growth rates, age structure, and mortality in fish and invertebrate populations (Ricker, 1975; Hilborn and Walters, 1992). The development of computer software for the analysis of length-frequency data has resulted in a rapid increase in the use of this technique (Pauly and Morgan, 1987; Terceiro et al., 1992). Length-frequency analysis relies on the assumption that length frequencies have modes, each of which represent a single age class. The modes are usually most distinct at young ages. When the modes are identified, the mean length of each age class in a population can be determined, and growth models may be fit to the lengths-at-age data. In most cases, the von Bertalanffy model has been used. Although a single sample of length frequencies may be analyzed in this manner, the evaluation of multiple, sequential samples from the same population allows a more powerful analysis by following modes through the samples in a time series.

Length-frequency analysis may be a useful approach to the study of growth in species other than fish and invertebrates. Recently, the accuracy of four length-frequency analysis programs (ELEFAN I, Shepherd's length composition analysis [SLCA], projection matrix method, and MULTIFAN) for predicting *number of age classes* (not ages) was tested in a population of green turtles in the southern Bahamas for which growth rates had been measured in a long-term mark and recapture study (Bjorndal and Bolten, 1995; Bjorndal et al., 1995). MULTIFAN successfully estimated the number of age classes in this population, SLCA was partially successful, ELEFAN I and the projection matrix method were not successful.

All of these length-frequency analysis programs solve for the set of von Bertalanffy growth parameters that yields the best description of the length distributions. A general form of the von Bertalanffy model is:

$$L_t = L_\infty(1 - e^{-K(t-t_0)})$$

where L_t is length at age t, L_∞ is asymptotic length, e is the base of the natural logarithms, K is an intrinsic growth rate variable, and t_0 is the nominal time that length is zero. However, because the four length-frequency programs employ different analytical approaches, the ability of each program to generate accurate growth models will vary for species with different life history strategies.

ELEFAN I (Electronic LEngth Frequency ANalysis) first restructures the length distributions by assigning positive values to length classes containing many animals and small or negative values to length classes with few animals (Pauly, 1987). Goodness of fit scores are then calculated by summing the values of the length classes through which each growth curve passes. An accurate growth curve will pass through length classes (or modes) with large numbers of animals and thus will accumulate a high goodness of fit score. The growth curve with the highest score is considered to be the best estimate.

As in ELEFAN, SLCA is based on the goodness of fit of the location of modes expected from a von Bertalanffy growth curve to the observed modes in the length distribution. However, length distributions are not restructured as in ELEFAN, and the goodness of fit criterion in SLCA is similar to that used in time series analysis (complex demodulation) (Shepherd, 1987a).

The projection matrix method was first developed as a method for forecasting short term catch-rates based on a combination of a time series of length compositions and estimates of growth parameters (Shepherd, 1987b). Rosenberg et al. (1986) adapted the method for estimating growth parameters. In this method, proportions in length classes are projected through time as predicted by a set of growth parameters. Expected length frequencies are generated and compared with a series of observed length frequencies, and an unweighted least squares objective function is used to determine the set of growth parameters that yield the best goodness of fit.

The MULTIFAN program integrates a nonlinear parameter estimation technique and maximum likelihood method to estimate the number of significant age classes in the sample population and the parameters of the von Bertalanffy growth model (Fournier et al., 1990, 1991).

In this study, only MULTIFAN was able to distinguish a global minimum among the many local minima of the objective functions and thus generate a best fit based on maximum likelihood values and corresponding estimates of the von Bertalanffy growth model parameters. The failure of the other three programs is not surprising, given their poorer performance with the Inagua green turtle data set (Bjorndal and Bolten, 1995). As discussed below, the Inagua data set was composed of a series of samples with more restricted geographic and temporal range, and thus would be expected to have less obscured age-class modes. Therefore, the rest of this report presents the results of the MULTIFAN analyses.

The MULTIFAN length-frequency program has the assumptions that

(1) growth is described by a von Bertalanffy growth curve,

(2) samples represent the structure of the population,

(3) recruitment occurs in seasonal pulses,

(4) the lengths of animals in each age class are normally distributed around the mean length, and

(5) the standard deviations of the actual lengths about the mean length-at-age are a simple function of the mean length-at-age.

MULTIFAN simultaneously analyzes multiple samples of length-frequency data. It uses nonlinear statistical modeling and robust parameter estimation to provide estimates of the parameters of the von Bertalanffy growth function. Log-likelihood objective functions are compared using maximum likelihood analyses to determine the model with the best fit.

The form of the von Bertalanffy equation that is used in the MULTIFAN program is

$$\mu_{j\alpha} = m_1 + (m_N - m_1)\left(\frac{1 - \rho^{j+(m(\alpha)-1)/12}}{1 - \rho^{N_j}}\right)$$

where $\mu_{j\alpha}$ is the mean length of the age class j turtles in the αth length frequency data set, m_1 is the mean length of the first age class, m_N is the mean length of the last age class, ρ is the Brody growth coefficient, $m(\alpha)$ - 1 is the number of months after the presumed birth month of the turtle in the αth length frequency data set, and N_j is the number of age classes in the data set. This parameterization of the von Bertalanffy growth equation is derived in Schnute and Fournier (1980).

The hundreds of sea turtles that strand on U.S. beaches each year are a source of data for length-frequency analysis. Data collected from turtles stranded in Georgia, Florida, Alabama, Mississippi, Louisiana and Texas were used in this study. Use of these data for length-frequency analyses is based on the assumption that the size distribution of stranded sea turtles represents the size distribution of sea turtles inhabiting coastal waters.

METHODS

Length-frequency Data

Volunteers monitor the shoreline and record data on each stranded sea turtle, including date and location of stranding, species, and carapace length (curved and/or straight carapace length). The data are compiled and archived at the Southeast Fisheries Science Center (SEFSC) Miami Laboratory (Teas, 1993a,b). We received data on stranded turtles for 1980 through 1995 for Georgia, Alabama, Mississippi, Louisiana and Texas from SEFSC. We received data for 1988 through 1995 for Florida from Florida Department of

Environmental Protection. All turtles known to have been head-started were excluded from the analyses.

Because most of the carapace length data were based on over-the-curve measurements, straight carapace lengths (SCL) were converted to curved carapace lengths (CCL). After conversions were completed, all CCL data were rounded to the nearest cm. The conversion equation used for loggerheads was from Teas (1993a):

$$SCL = (0.948 \times CCL) - 1.442$$

Sample size was 932, and linear regression yielded an R^2 of 0.97 and $P < 0.001$.

Because the conversion equations presented by Teas (1993a) for Kemp's ridleys and green turtles were based on small samples sizes, conversion equations for these two species were generated from the data set using values for those turtles for which both straight and curved measurements had been taken. For Kemp's ridleys, the conversion equation was:

$$CCL = (1.044 \times SCL) + 0.607$$

Sample size was 812, range of SCL was from 18.0 to 67.6 cm, and linear regression yielded an R^2 of 0.994 and $P < 0.001$.

For green turtles, the conversion equation was:

$$CCL = (1.061 \times SCL) + 0.079$$

Sample size was 635 green turtles that stranded on the Florida Atlantic coast, range of SCL was from 20.0 to 113.5 cm, and linear regression yielded an R^2 of 0.996 and $P < 0.001$.

Loggerheads

The size distribution for the total database for loggerheads between 46 and 87 cm CCL is shown in Figure 1. The loggerhead size range for length-frequency analyses was limited to the sub-adult, benthic lifestage: 46-87 cm CCL. The lower value was based on the size distributions in Bolten et al. (1993) that indicated that 46 cm CCL is the beginning of the benthic juvenile stage. The largest sub-adult size was taken as 87 cm CCL based on Witherington (1986), who reported that 88 cm CCL was the size of the smallest nesting loggerhead at Melbourne Beach, Florida. We used a very conservative cut-off between sub-adults and adults for all three sea turtle species. Certainly, many loggerheads with CCL greater than 87 cm are still immature. For these analyses, however, it is better to exclude some sub-adults than include many adult animals. Any factor that acts to obscure the modal structure of the sample will decrease the potential for successful length-frequency analysis. Such factors include cessation or near-cessation of growth in older age classes. If older age classes cannot be distinguished, K will be overestimated and the number of age classes underestimated (Terceiro et al., 1992). Because sea turtles essentially stop growing at sexual maturity and because they attain sexual maturity at a range of sizes, the age classes--or modes--above the minimum size at sexual maturity are obscured and cannot be distinguished in length-frequency analyses.

The loggerhead stranding data were divided into the following subsets for length-frequency analyses:

(1) Florida Atlantic 1988-1995

(2) Florida Gulf 1988-1995

(3) Georgia 1980-1995

(4) Georgia 1980-1987

(5) Georgia 1988-1995

(6) Florida Atlantic and Georgia 1988-1995

(7) Texas 1980-1995

(8) Texas 1980-1987

(9) Texas 1988-1995

(10) Gulf 1988-1995, which included Texas, Louisiana, Mississippi, Alabama and Florida Gulf

The data sets were divided between 1980-1987 and 1988-1995 because only data from 1988 through 1995 were available for Florida.

Kemp's ridleys

For Kemp's ridleys, the size distribution for length-frequency analyses was limited to the sub-adult, benthic lifestage: 20-61 cm CCL (Figure 2). The lowest value of 20 cm represents the smallest size at which the size distribution becomes continuous. The largest sub-adult size was set at 61 cm CCL because Márquez-M. (1994) gave 58.5 cm as the mean minimum SCL of nesting Kemp's ridleys for 1966 to 1992. We converted 58.5 cm SCL to 61.7 cm CCL using the conversion equation given above. The 61.7 cm value was rounded to 62 cm, giving 61 cm as the largest sub-adult size.

The Kemp's ridley stranding data were divided into the following subsets for length-frequency analyses:

(1) Total 1988-1995, which included Georgia, Florida, Alabama, Mississippi, Louisiana and Texas

(2) Gulf 1988-1995, which included the Gulf coast of Florida, Alabama, Mississippi, Louisiana and Texas

(3) Atlantic 1988-1995, which included the Atlantic coast of Florida and Georgia

Green turtles

The size range for length-frequency analyses for green turtles was limited from 25 to 70 cm CCL. This range does not represent the size range of sub-adult benthic green turtles. Rather, it represents the continuous size range of green turtles represented in the stranding database. Length-frequency analyses can only be conducted on continuous size distributions. Green turtles in the size range of large sub-adults are rare in the stranding data, and, presumably, are not found in significant numbers in the waters of the southeastern United States.

The only sample used in length-frequency analyses for green turtles was the turtles that stranded along the Atlantic coast of Florida from 1988 through 1995 (Figure 3). The sample sizes in other regions were too small for length-frequency analysis.

Length-frequency Analysis

The length-frequency analysis programs were obtained from two sources. ELEFAN I, Shepherd's length composition analysis, and projection matrix were from the Length Frequency Distribution Analysis Package (version 3.10) produced by Marine Resources Assessment Group Limited with support from the British Overseas Development Administration (Holden and Bravington, 1992). MULTIFAN was version 32(f) modified to include 30 age classes by Fournier (October 1996, pers. comm.). MULTIFAN is produced by Otter Research Ltd., Nanaimo, B.C., Canada (Otter Research Ltd., 1992).

MULTIFAN requires that initial values for the following parameters be specified as starting points for the iterations: expected number of age classes, expected initial K values, mean length of the mode representing the youngest age class, standard deviation of a distinct mode, and month in which youngest animals recruit to the population. We estimated initial values for age classes as varying between 2 and 30 years, and for K as 0.01, 0.05, 0.1, and 0.5. The mean length of youngest age class varied with species and populations within species. The initial standard deviation of mode width was estimated as 1.5 (Fournier, pers. comm.). Because initial MULTIFAN runs indicated that there was a significant trend in standard deviation of length-at-age with increasing length, this parameter was included in the model for all analyses reported here. Iterations were run in which March, April, May or June were evaluated as the month of recruitment into the population.

We attempted to use data for individual months in each year, but initial analyses indicated that sample sizes were too small. As a result, data were combined for each month among years for each of the three species. Even after data were combined among years, some months still had to be dropped from analyses because of small sample size. We employed a generally accepted rule-of-thumb that sample size should be at least 1 or 2 times the number of size increments in the distribution. For example, for green turtles with a size range of 25 to 70 cm at 1 cm increments required a minimum sample size of 45 to 90 green turtles.

RESULTS AND DISCUSSION

Loggerheads

We ran a series of 27 analyses with MULTIFAN software using different combinations of database subsamples, initial parameter estimates, and designated month of recruitment. Each of the 27 analyses consisted of three runs: initial analysis, analysis in which standard deviations of modes were allowed to vary, and analysis in which K was allowed to vary. The first analyses used individual month samples without combining among years, for Florida, Georgia and Texas. It quickly became clear that the samples were too small to be representative of the size distribution of sea turtles in those areas. At that point we combined month samples among years.

We then worked with loggerheads that had stranded along the Atlantic coast of Florida (= Florida Atlantic) from 1988 through 1995 (Figure 4). We considered this sample to have the best potential for distinct modal structure because of its restricted geographic range and the efforts of Barbara Schroeder to identify and discard questionable data. Note that the size distribution in Figure 4 is very similar to that of all loggerheads in Figure 1. This analysis indicated that loggerheads require 20 years to grow from 46 to 87 cm CCL (Table 1; Figure 5). The von Bertalanffy equation is:

$$\mu_{j\alpha} = 44.1 + (86.5 - 44.1)\left(\frac{1 - 0.957^{j+(m(\alpha)-1)/12}}{1 - 0.957^{20}}\right)$$

The length-frequency distributions for the combined-month samples and the age-class modes fitted to the distributions by MULTIFAN are shown in Figure 6.

Next, we determined whether length-frequency analysis of loggerheads in the Gulf of Mexico would yield different results from those of Florida Atlantic loggerheads. We first worked with the subsample of loggerheads that had stranded in Texas from 1980 through 1995 (Figure 7). We selected this subsample because it had a relatively restricted geographic range with sufficiently large sample sizes. This analysis generated an estimate of an 18 year interval between 46 and 87 cm CCL for Texas loggerheads (Table 1; Figure 8), but the estimate for the asymptote (L_∞) was much higher at 144 cm. The poor estimate may be a result of the large number of years combined in the Texas sample. The von Bertalanffy equation is:

$$\mu_{j\alpha} = 47.4 + (86.2 - 47.4)\left(\frac{1 - 0.970^{j+(m(\alpha)-1)/12}}{1 - 0.970^{18}}\right)$$

The length-frequency distributions for the combined-month samples and the age-class modes fitted to the distributions by MULTIFAN are shown in Figure 9.

To decrease the number of years and still have sufficiently large samples, we combined data for loggerhead strandings in the Gulf of Mexico from 1988 through 1995 (Figure 10). These years were used because data from the Gulf coast of Florida were only available for these years. This subsample included loggerheads that stranded in Texas, Louisiana, Mississippi, Alabama, and the Gulf coast of Florida. MULTIFAN analysis of the Gulf of Mexico sample yielded values similar to the Florida Atlantic sample: 20-year interval to grow from 46 to 87 cm, and an asymptote of 113 cm CCL (Table 1; Figure 11). The von Bertalanffy equation is:

$$\mu_{j\alpha} = 43.3 + (86.8 - 43.3)\left(\frac{1 - 0.950^{j+(m(\alpha)-1)/12}}{1 - 0.950^{20}}\right)$$

The length-frequency distributions for the combined-month samples and the age-class modes fitted to the distributions by MULTIFAN are shown in Figure 12.

The rest of the analyses were attempts to modify the model to determine if such modifications would improve the performance of the models. Based on statistical comparisons of maximum likelihood functions using chi square tests, none of the modifications significantly improved the models.

Thus, the best fits from our length-frequency loggerhead analyses are presented in Table 1 for the Florida Atlantic and Gulf of Mexico subsamples. Estimates of von Bertalanffy model parameters from other studies for loggerheads captured on the Atlantic coast of Florida, were 95 cm SCL asymptotic size and 0.12 for K (Frazer and Ehrhart, 1985) and 96 cm SCL asymptotic size and K equal to 0.06 (Schmid, 1995). These estimates are not substantially different from our estimates for Florida Atlantic loggerheads, except the K value from Frazer and Ehrhart (1985) is about three times higher (Table 1).

MULTIFAN also calculates the age of the first size class in the sample, based on the von Bertalanffy model that it selects as the best fit. This estimate--reported in Table 1 in the column headed "First Age"--is 10.5 years for the Florida Atlantic sample and 9.4 years for the Gulf of Mexico sample. One could add this estimate to the estimate of number of age classes between 46 and 87 cm and derive an estimate of the age of loggerheads with a CCL of 87 cm: 30.5 years for the Florida Atlantic sample and 29.4 years for the Gulf of Mexico sample. As discussed in more detail below, this use of the estimate of the age of the first size class in the sample is inappropriate because it requires an extrapolation outside of the database and is based on the assumption that loggerhead growth follows a von Bertalanffy curve throughout all life stages--an assumption for which we have no data to support.

This estimate of age at 87 cm CCL should not be used as an estimate of age to sexual maturity. Although we used 87 cm CCL to represent the largest sub-adult loggerhead in this study, as explained above, we used a conservative estimate to exclude almost all adult loggerheads from the sample to exclude obscured modes from our size distributions. Many loggerheads will reach sexual maturity at lengths much greater than 87 cm CCL, and, because growth rates are slow in these large sub-adults, the average age to sexual maturity would be substantially greater than the average age to 87 cm CCL.

Kemp's Ridleys

We ran a series of 10 analyses with MULTIFAN software using different combinations of database subsamples, initial parameter estimates, and designated month of recruitment. Each of the 10 analyses consisted of three runs: initial analysis, analysis in which standard deviations of modes were allowed to vary, and analysis in which K was allowed to vary. The first analyses were based on the total database (Figure 2), including Kemp's ridleys stranded in the Georgia, Florida, Alabama, Mississippi, Louisiana and Texas from 1988 through 1995. Estimates of asymptotic size generated for this data set were unacceptably high (160 to 714 cm). The poor performance of MULTIFAN with this sample may have been a result of combining samples from a wide geographic range that may have obscured modes in the size distributions. Any variation in individual growth rates that result in variation in length-at-age will obscure age-class modes and reduce the ability of length-frequency analyses to accurately distinguish age-class modes. Some of the most common causes of variation in individual growth rates are differences in temperature and food availability. Thus, by combining samples over a broad geographic areas, great variation in temperature regimes and food resources are incorporated in the sample.

The next analyses used the data for Kemp's ridleys stranded in the Gulf of Mexico (Figure 13); the sample sizes for the Atlantic coast (Georgia and Florida; Figure 14) were too small. In Table 1, we present the set of estimates generated by MULTIFAN with the best fit, as judged from the maximum value of the log-likelihood function value for the Gulf of Mexico sample. An estimated 15 years are required for a Kemp's ridley to grow from 20 cm to 61 cm CCL (Figure 15). The von Bertalanffy equation is:

$$\mu_{j\alpha} = 21.1 + (60.7 - 21.1)\left(\frac{1 - 0.949^{j+(m(\alpha)-1)/12}}{1 - 0.949^{15}}\right)$$

The length-frequency distributions for the combined-month samples and the age-class modes fitted to the distributions by MULTIFAN are shown in Figure 16.

Estimates of von Bertalanffy model parameters for Kemp's ridleys captured in Cape Canaveral, Florida, varied between 61 and 78 cm SCL for asymptotic size and between 0.05 and 0.60 for K (Schmid, 1995). Our estimate for asymptotic size is above this range, but our estimate for K falls within this range (Table 1). Estimates for von Bertalanffy growth parameters calculated for post-release head-started Kemp's ridleys in the Gulf of Mexico were 62 cm SCL for asymptotic size and 0.32 for K (Caillouet et al., 1995). This asymptote estimate is smaller and the K estimate is higher than our estimated values.

The caveats given above in the loggerhead discussion section regarding the use of the age of first size class and estimates of age to sexual maturity apply equally well to the Kemp's ridley estimates.

Green Turtles

We ran a series of five analyses with MULTIFAN software using different combinations of database subsamples, initial parameter estimates, and designated month of recruitment. Each of the five analyses consisted of three runs: initial analysis, analysis in which standard deviations of modes were allowed to vary, and analysis in which K was allowed to vary. The only sample we attempted to analyze for green turtles was those stranded on the Atlantic coast of Florida because the sample sizes from other areas were very small.

The best results as judged from the maximum value of the log-likelihood function value for the Florida Atlantic green turtles are given in Table 1. The von Bertalanffy equation is:

$$\mu_{j\alpha} = 25.8 + (67.3 - 25.8)\left(\frac{1 - 0.975^{j+(m(\alpha)-1)/12}}{1 - 0.975^{13}}\right)$$

MULTIFAN generated an estimate of 13 years as the time required for a green turtle to grow from 25 to 70 cm CCL (Figure 17). The length-frequency distributions for the combined-month samples and the age-class modes fitted to the distributions by MULTIFAN are shown in Figure 18.

The estimate of 13 years is similar to that presented for Florida green turtles in Frazer and Ehrhart (1985). Growth over a similar size range in green turtles in the southern Bahamas was estimated by the MULTIFAN length-frequency analysis to require 11 years (Bjorndal and Bolten, 1995; Bjorndal et al., 1995). This more rapid growth rate would be expected in warmer waters. The estimate of asymptotic length (182 cm CCL) given in Table 1 is high. We believe that the overestimate for the asymptote is a result of the paucity of large sub-adults in the Florida sample (Figure 3). Frazer et al. (1990) demonstrated that removal of large individuals from a sample of freshwater turtles resulted in poor estimation of asymptotic size in von Bertalanffy models.

The warning given above in the loggerhead discussion section regarding the use of the age of first size class and estimates of age to sexual maturity also applies to the green turtle estimates.

Limitations of Length-frequency Analyses

Just as sea turtles have characteristics that make them challenging subjects for mark and recapture studies (see Introduction), populations of sea turtles also have characteristics that can make the use of length-frequency analysis problematic. Any factor that obscures modal structure makes length-frequency analysis more difficult. Such factors include long spawning season, variation in individual growth rates that result in variation in length-at-age, cessation or near cessation of growth in old age classes, and high rates of exploitation. If older age classes cannot be distinguished, K will be overestimated and the number of age classes will be underestimated (Terceiro et al., 1992). If length-frequency data sets are drawn from a wide geographic region, variation in growth rates over that region may result in obscured modal structure. Also, populations with very high exploitation may have reduced modal structure at the largest sizes, which will result in overestimates of K and underestimates of number of age classes (Terceiro et al., 1992).

In addition to these general problems with the application of length-frequency analyses to sea turtles, the stranding data set has two problems. First, the samples are not clearly differentiated. The stranding of sea turtles, and therefore the sampling, was continual over the study period and arbitrarily separated into months. Thus, a turtle that stranded on 31 March was placed in the March sample, although it is biologically more similar to a turtle that stranded on 1 April than to one that stranded on 1 March. Further contamination of monthly samples no doubt occurred as a result of the time lag between death and stranding of some carcasses. That is, a turtle that died in the third week of June but did not wash ashore until July would be included in the July sample although it should have been in the June sample. This lack of clearly defined samples is in contrast to the Bahamian green turtle samples on which MULTIFAN was tested (Bjorndal and Bolten, 1995; Bjorndal et al., 1995); those samples were based on live turtles captured during discrete 2-week intervals.

The second problem with the stranding database is a result of small sample size, which required that we combine months from different years. Because of annual variations in water temperatures in these temperate habitats, one would predict that growth rates in each month would vary between years (particularly in spring and fall months when temperatures are most variable from year to year) and that combining samples among years would therefore tend to obscure modes.

A concern with length-frequency analyses that is not limited to sea turtles is use of the von Bertalanffy model in almost all such analyses (Chaloupka and Musick, 1997). As has been discussed for nonlinear regression analysis of turtle growth data (Bjorndal and Bolten, 1988; Boulon and Frazer, 1990; Frazer et al., 1990; Chaloupka and Musick, 1997), extrapolating beyond the size range included in the study may yield unreliable results in length-frequency analysis. At present, it is not known whether the von Bertalanffy model is appropriate for these three species of sea turtles, but studies in Australia (Chaloupka and Limpus, 1997; Limpus and Chaloupka, in press) and in the Atlantic (Chaloupka and Zug, in review; Bjorndal, Bolten and Chaloupka, in preparation) indicate that the von Bertalanffy model is not appropriate for some populations of sea turtles. As growth data accumulate for Atlantic sea turtle populations, appropriate growth curves can be determined and incorporated into the length-frequency software.

ACKNOWLEDGEMENTS

This project could not have been conducted without the long hours invested by the many volunteers in the Sea Turtle Stranding and Salvage Network. Support for this project was provided by the MARFIN program of the National Marine Fisheries Service (project NA57FF0063). We thank Wayne Witzell and Nancy Thompson for their assistance with this project. David Fournier generously provided advice and modification of the MULTIFAN software. Peter Eliazar assisted with data compilation, and Laurie Walz drafted the figures.

LITERATURE CITED

Balazs, G. H. 1982. Growth rates of immature green turtles in the Hawaiian Archipelago. Pages 117-125 in K. A. Bjorndal (editor), Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Washington, D.C.

Bjorndal, K. A., and A. B. Bolten. 1988. Growth rates of immature green turtles, *Chelonia mydas*, on feeding grounds in the southern Bahamas. Copeia 1988:555-564.

Bjorndal, K. A., and A. B. Bolten. 1995. Comparison of length-frequency analyses for estimation of growth parameters for a population of green turtles. Herpetologica 51:160-167.

Bjorndal, K. A., A. B. Bolten, A. L. Coan, Jr., and P. Kleiber. 1995. Estimation of green turtle (*Chelonia mydas*) growth rates from length-frequency analysis. Copeia 1995:71-77.

Bolten, A. B., H. R. Martins, K. A. Bjorndal, and J. Gordon. 1993. Size distribution of pelagic-stage loggerhead sea turtles (*Caretta caretta*) in the waters around the Azores and Madeira. Arquipélago 11A:49-54.

Boulon, R. H., Jr., and N. B. Frazer. 1990. Growth of wild juvenile Caribbean green turtles, *Chelonia mydas*. Journal of Herpetology 24:441-445.

Caillouet, C. W., Jr., C. T. Fontaine, S. A. Manzella-Tirpak, and T. D. Williams. 1995. Growth of head-started Kemp's ridley sea turtles (*Lepidochelys kempii*) following release. Chelonian Conservation and Biology 1:231-234.

Chaloupka, M. Y., and C. J. Limpus. 1997. Robust statistical modelling of hawksbill sea turtle growth rates (southern Great Barrier Reef). Marine Ecology Progress Series 146:1-8.

Chaloupka, M. Y., and J. A. Musick. 1997. Age, growth, and populations dynamics. Pages 233-276 in P. L. Lutz and J. A. Musick (editors), The Biology of Sea Turtles. CRC Press, Boca Raton, FL.

Fournier, D. A., J. R. Sibert, J. Majkowski, and J. Hampton. 1990. MULTIFAN, a likelihood-based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for southern bluefin tuna (*Thunnus maccoyii*). Canadian Journal of Fisheries and Aquatic Sciences 47:301-317.

Fournier, D. A., J. R. Sibert, and M. Terceiro. 1991. Analysis of length frequency samples with relative abundance data for the Gulf of Maine northern shrimp (*Pandalus borealis*) by the MULTIFAN method. Canadian Journal of Fisheries and Aquatic Sciences 48:591-598.

Frazer, N. B., and L. M. Ehrhart. 1985. Preliminary growth models for green, *Chelonia mydas*, and loggerhead, *Caretta caretta*, turtles in the wild. Copeia 1985:73-79.

Frazer, N. B., J. W. Gibbons, and J. L. Greene. 1990. Exploring Fabens' growth interval model with data on a long-lived vertebrate, *Trachemys scripta* (Reptilia: Testudinata). Copeia 1990:112-118.

Hilborn, R., and C. J. Walters. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, New York.

Holden, S., and M. Bravington. 1992. Length Frequency Distribution Analysis, the LFDA Package user manual, version 3.10. Marine Resources Assessment Group Limited, London.

Limpus, C. J. 1992. The hawksbill turtle, *Eretmochelys imbricata*, in Queensland: Population structure within a southern Great Barrier Reef feeding ground. Wildlife Research 19:489-506.

Limpus, C. and M. Chaloupka. In press. Nonparametric regression modelling of green sea turtle growth rates (southern Great Barrier Reef). Marine Ecology Progress Series.

Márquez-M., R. 1994. Sinopsis de datos biologicos sobre la tortuga lora, *Lepidochelys kempi* (Garman, 1880). FAO Sinopsis sobre la Pesca, No. 152, 141 pages.

Otter Research Ltd. 1992. MULTIFAN 3 User's Guide and Reference Manual. Otter Research Ltd., Nanaimo, B.C., Canada.

Pauly, D. 1987. A review of the ELEFAN system for analysis of length-frequency data in fish and aquatic invertebrates. Pages 7-34 in D. Pauly and G. R. Morgan (editors), Length-based Methods in Fisheries Research. International Center for Living Aquatic Resources Management, Manila, Philippines.

Pauly, D., and G. R. Morgan (editors). 1987. Length-based methods in fisheries research. ICLARM Conference Proceedings, No. 13, ICLARM, Manila.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada, Bulletin No. 191.

Rosenberg, A. A., J. R. Beddington, and M. Basson. 1986. The growth and longevity of krill during the first decade of pelagic whaling. Nature 324:152-154.

Schnute, J., and D. A. Fournier. 1980. A new approach to length frequency analysis: growth structure. Journal of the Fisheries Research Board of Canada 37:1337-1351.

Shepherd, J. G. 1987a. A weakly parametric method for estimating growth parameters from length composition data. Pages 113-119 in D. Pauly and G. R. Morgan (editors), Length-based Methods in Fisheries Research. International Center for Living Aquatic Resources Management, Manila, Philippines.

Shepherd, J. G. 1987b. Towards a method for short-term forecasting of catch rates based on length compositions. Pages 167-176 in D. Pauly and G. R. Morgan (editors), Length-based Methods in Fisheries Research. International Center for Living Aquatic Resources Management, Manila, Philippines.

Schmid, J. R. 1995. Marine turtle populations on the east-central coast of Florida: results of tagging studies at Cape Canaveral, Florida, 1986-1991. Fishery Bulletin 93:139-151.

Teas, W. G. 1993a. Species composition and size class distribution of marine turtle strandings on the Gulf of Mexico and southeast United States coasts, 1985-1991. NOAA Technical Memorandum NMFS-SEFSC-315, 43 pages.

Teas, W. G. 1993b. 1992 annual report of the sea turtle stranding and salvage network, Atlantic and Gulf coasts of the United States, January-December 1992. NOAA

Southeast Fisheries Science Center Miami Laboratory Contribution Number MIA-92/93-73, 43 pages.

Terceiro, M., D. A. Fournier, and J. R. Sibert. 1992. Comparative performance of MULTIFAN and Shepherd's length composition analysis (SLCA) on simulated length-frequency distributions. Transactions of the American Fisheries Society 121:667-677.

Witherington, B. E. 1986. Human and natural causes of marine turtle clutch and hatchling mortality and their relationship to hatchling production on an important Florida nesting beach. Masters Thesis, University of Central Florida, Orlando.

Table 1. Results of length-frequency analyses using the software MULTIFAN for three species of sea turtles in the southeastern United States. Estimates for two parameters from the von Bertalanffy model are given: L_∞ is asymptotic length (CCL, cm) and K is an intrinsic growth rate variable. CCL is curved carapace length, initial month is month in which turtles recruited to the population, first age is age in years of first age class, n is sample size.

Sample	CCL Range (cm)	No. Age Classes (yrs)	L_∞	K	Initial Month	First Age (yrs)	n
Loggerheads							
Florida Atlantic 1988-1995	46-87	20	119	0.044	April	10.5	1234
Texas 1980-1995	46-87	18	144	0.030	April	13.2	819
Gulf of Mexico 1988-1995	46-87	20	113	0.051	April	9.4	570
Kemp's Ridleys							
Gulf of Mexico 1988-1995	20-61	15	97	0.053	May	4.7	660
Green Turtles							
Florida Atlantic 1988-1995	25-70	13	182	0.026	March	5.9	976

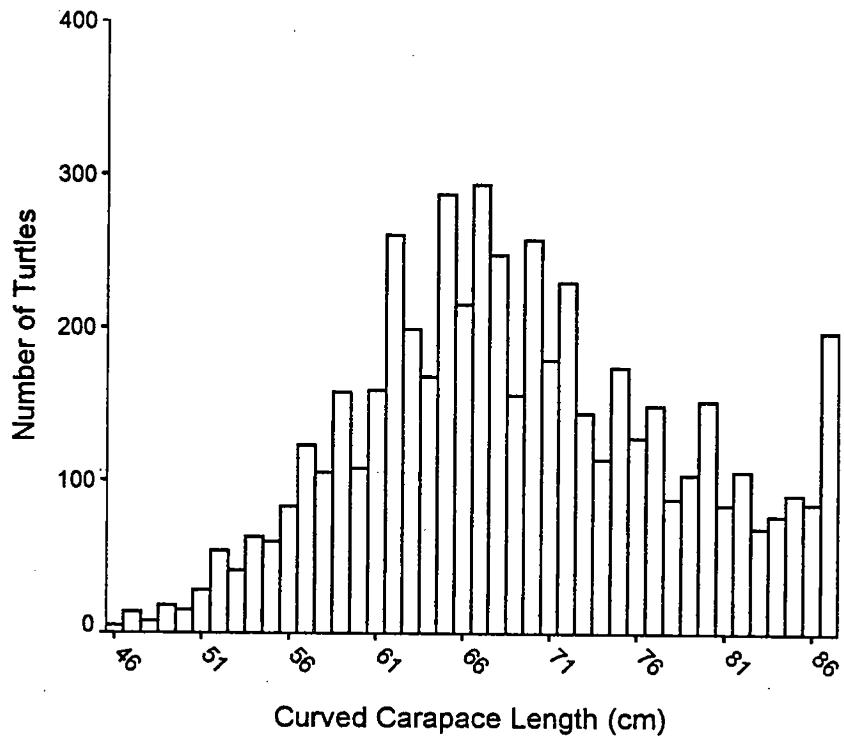


Figure 1. Size frequency of stranded loggerhead sea turtles (*Caretta caretta*) from 1980 through 1995 in Georgia, Alabama, Mississippi, Louisiana and Texas, and from 1988 through 1995 in Florida. The size range for length-frequency analyses was limited to the sub-adult, benthic lifestage of 46-87 cm curved carapace length.

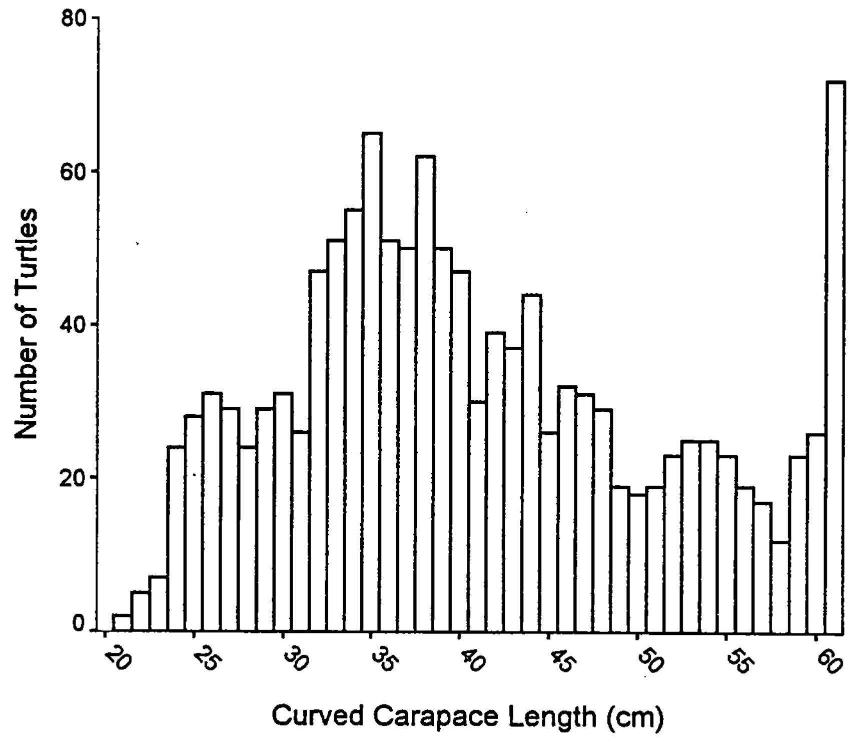


Figure 2. Size frequency of stranded Kemp's ridleys (*Lepidochelys kempi*) from 1988 through 1995 in Georgia, Florida, Alabama, Mississippi, Louisiana and Texas. The size range for length-frequency analyses was limited to the sub-adult, benthic lifestage of 20-61 cm curved carapace length.

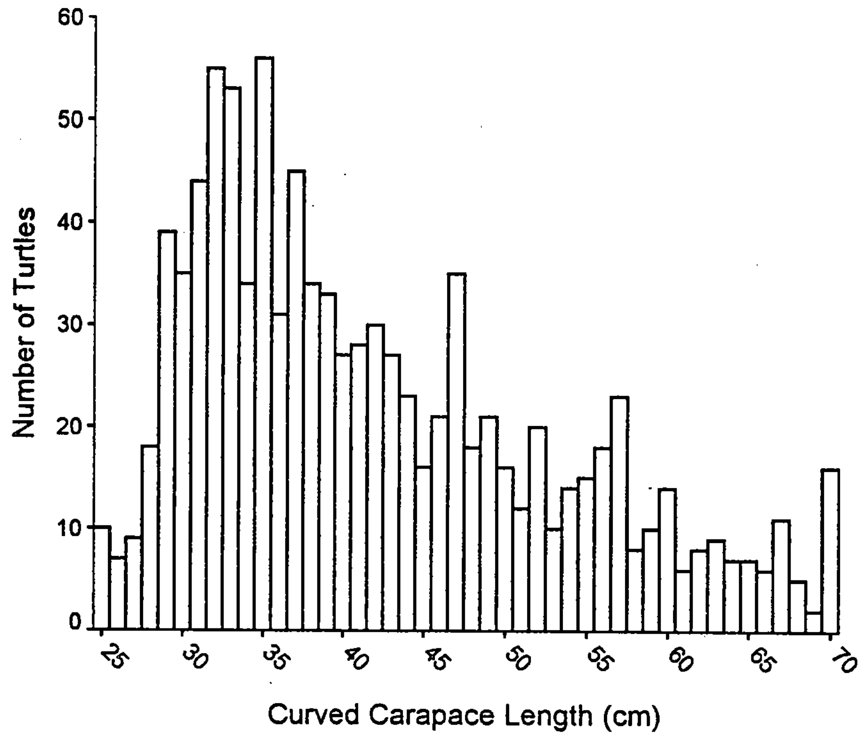


Figure 3. Size frequency of stranded green turtles (*Chelonia mydas*) from 1988 through 1995 along the Atlantic coast of Florida. The size range for length frequency analyses was limited to 25 to 70 cm curved carapace length.

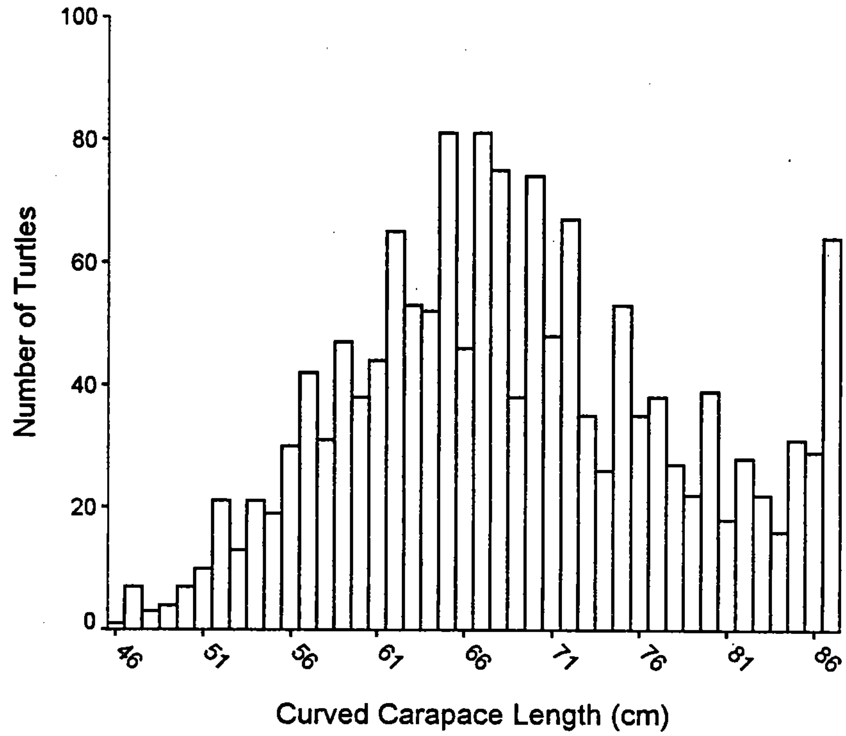


Figure 4. Size frequency of loggerhead sea turtles stranded along the Atlantic coast of Florida from 1988 through 1995 within the size range of 46 to 87 cm curved carapace length.

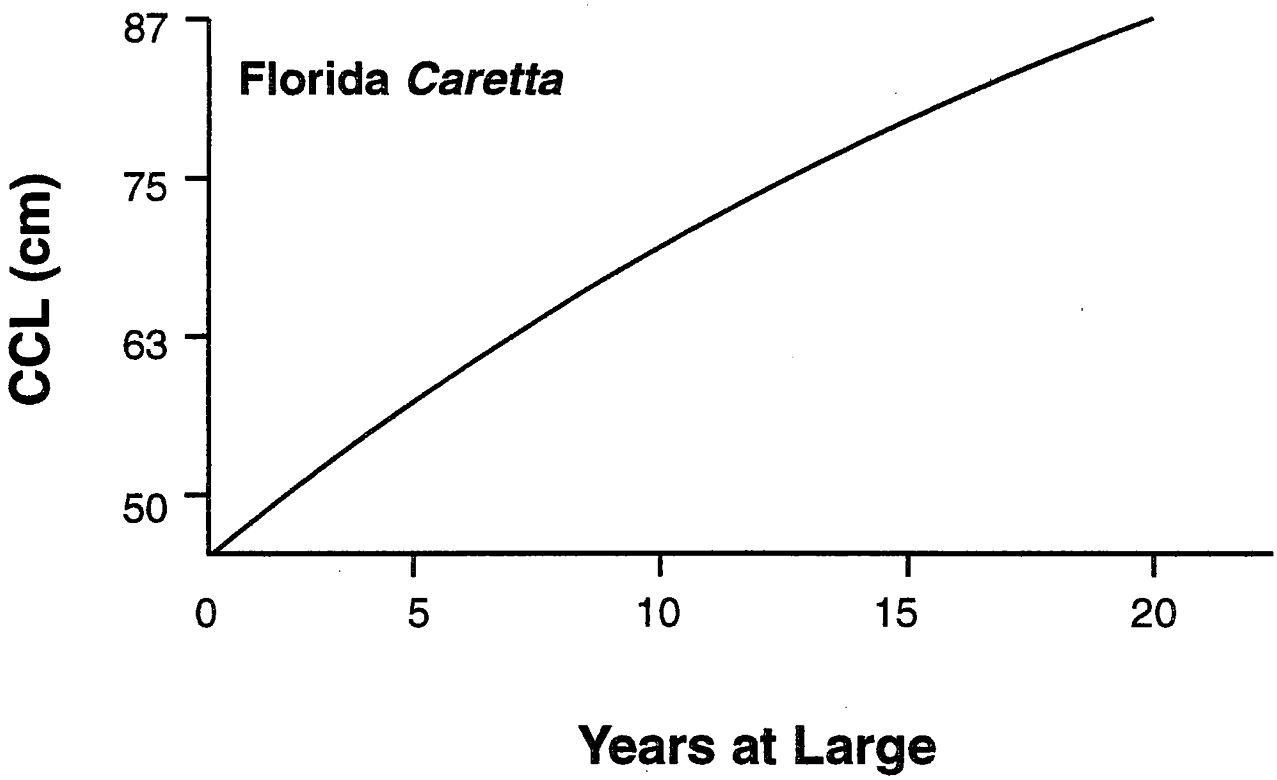
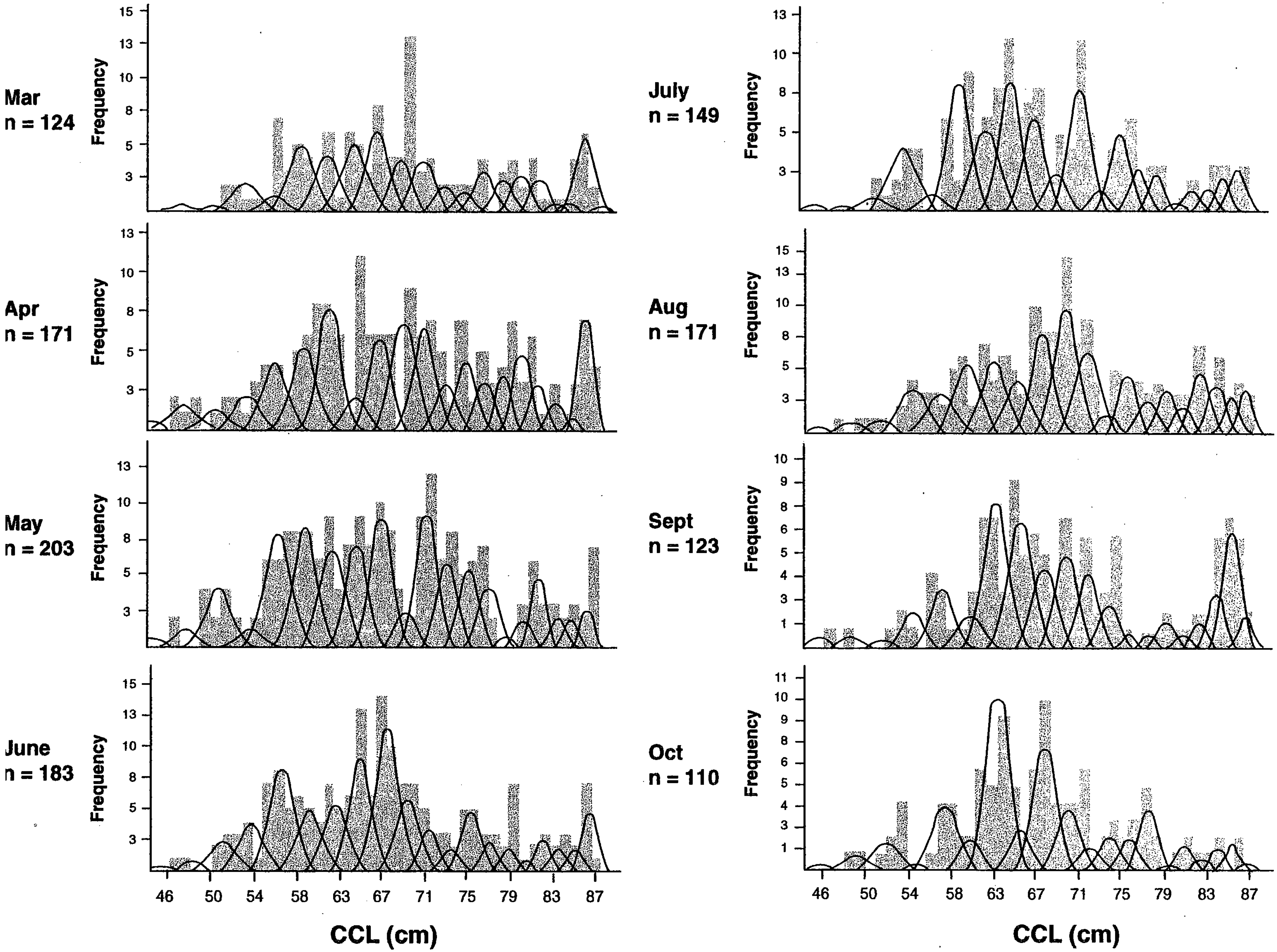


Figure 5. Von Bertalanffy growth model generated by MULTIFAN for loggerhead sea turtles stranded along the Atlantic coast of Florida from 1988 through 1995 within the size range of 46 to 87 cm curved carapace length. See text for equation.

Figure 6. Length-frequency distributions of combined-month samples for loggerhead sea turtles stranded along the Atlantic coast of Florida from 1988 through 1995 within the size range of 46 to 87 cm curved carapace length. Curves represent age-class modes assigned by MULTIFAN; midpoint of each mode indicates the mean CCL of each age class. Months not shown had samples that were too small to be representative of the population's length-frequency distribution, and thus were excluded from analyses.



Mar
n = 124
Apr
n = 171
May
n = 203
June
n = 183
July
n = 149
Aug
n = 171
Sept
n = 123
Oct
n = 110
Frequency
46 50 54 58 63 67 71 75 79 83 87
CCL (cm)

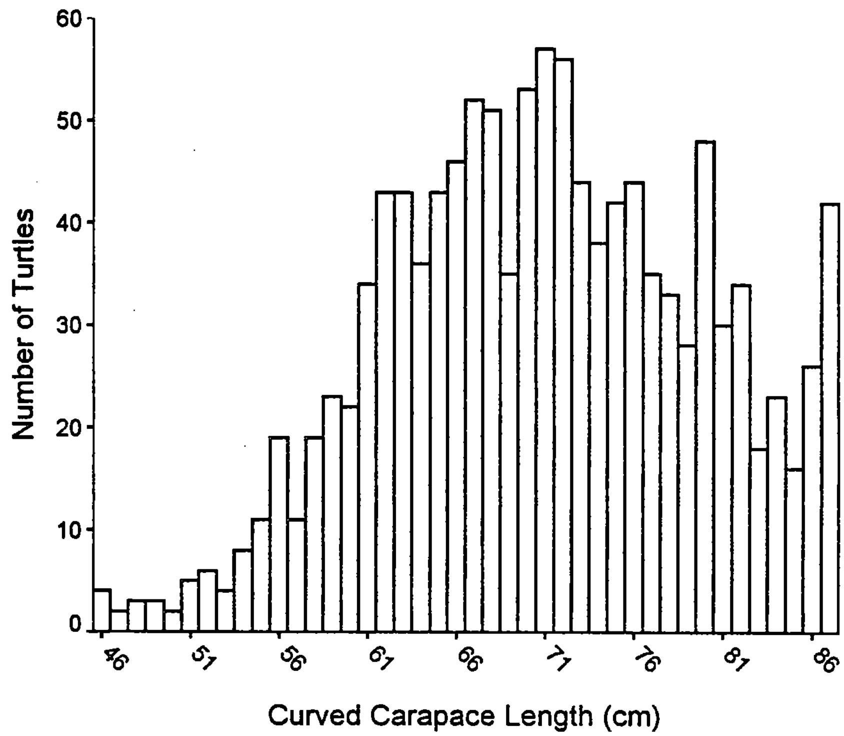


Figure 7. Size frequency of loggerhead sea turtles stranded in Texas from 1980 through 1995 within the size range of 46 to 87 cm curved carapace length.

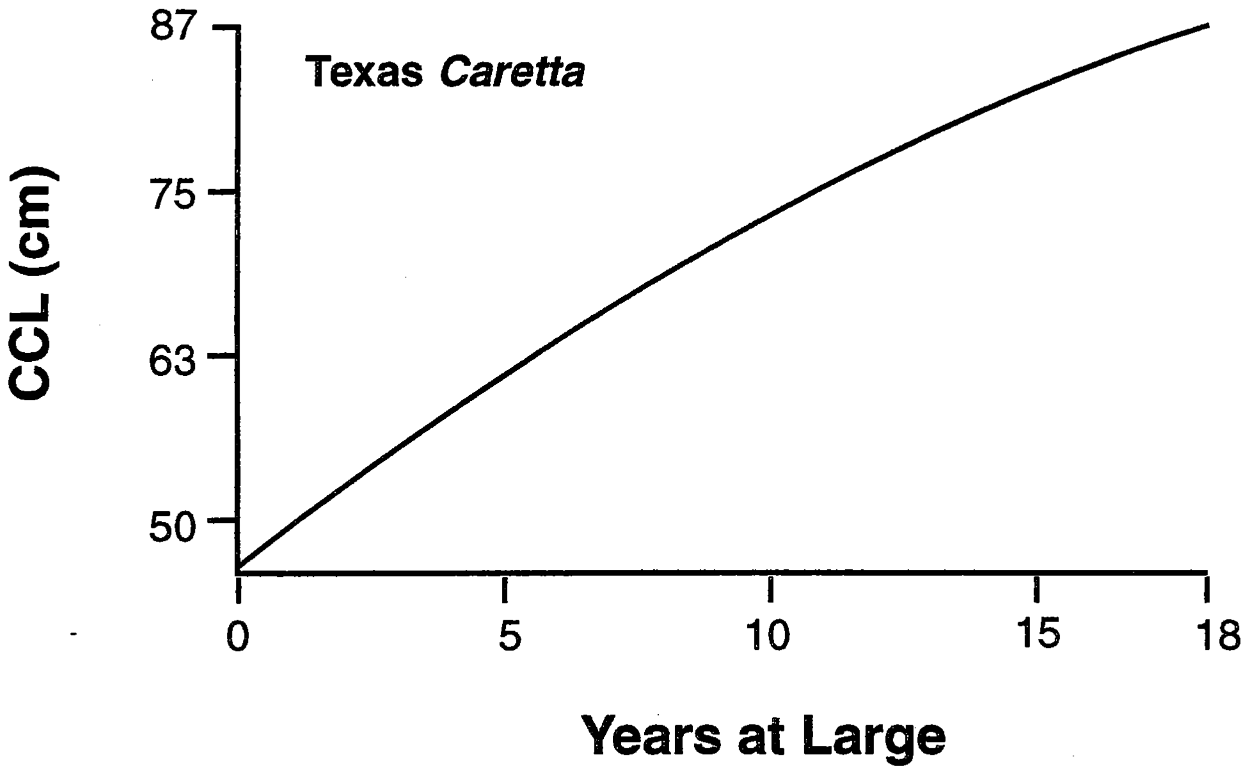
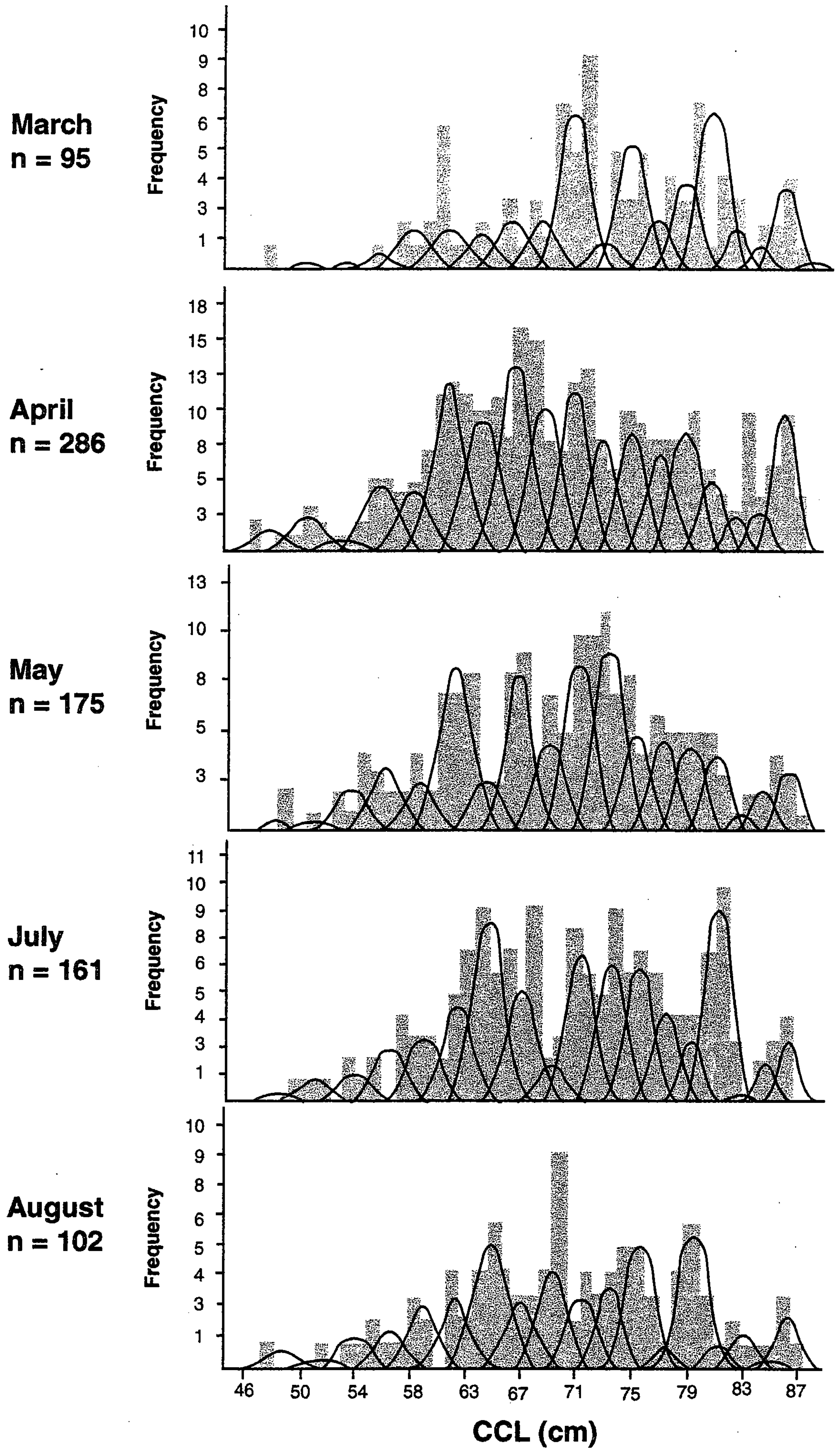


Figure 8. Von Bertalanffy growth model generated by MULTIFAN for loggerhead sea turtles stranded along the Texas coast from 1980 through 1995 within the size range of 46 to 87 cm curved carapace length. See text for equation.

Figure 9. Length-frequency distributions of combined-month samples for loggerhead sea turtles stranded along the Texas coast from 1980 through 1995 within the size range of 46 to 87 cm curved carapace length. Curves represent age-class modes assigned by MULTIFAN; midpoint of each mode indicates the mean CCL of each age class. Months not shown had samples that were too small to be representative of the population's length-frequency distribution, and thus were excluded from analyses.



March
n = 95
April
n = 286
May
n = 175
July
n = 161
August
n = 102
Frequency
46
50
54
58
63
67
71
75
79
83
87
CCL (cm)

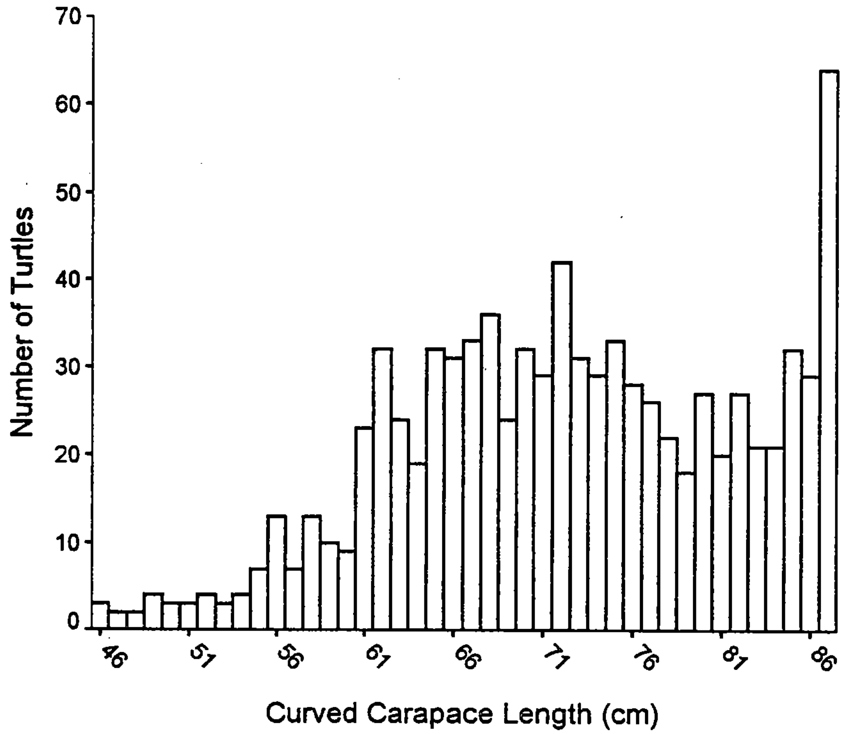


Figure 10. Size frequency of loggerhead sea turtles stranded in the Gulf of Mexico from 1988 through 1995 within the size range of 46 to 87 cm curved carapace length.

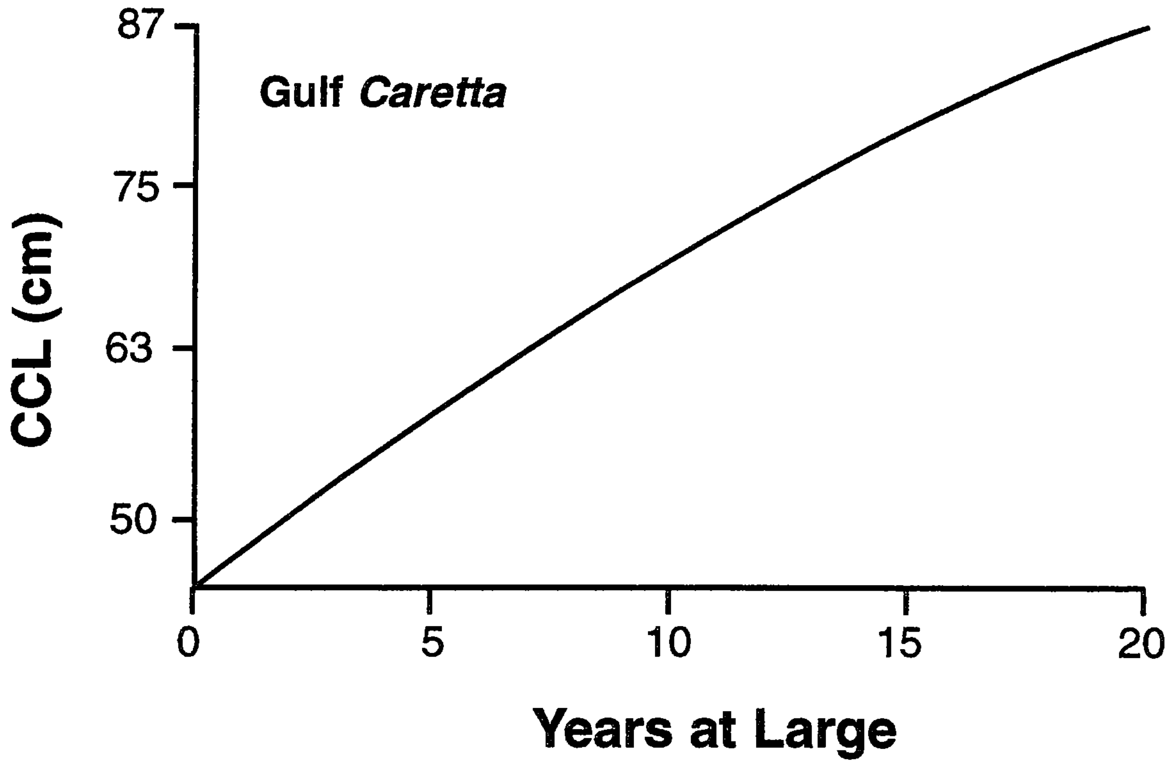
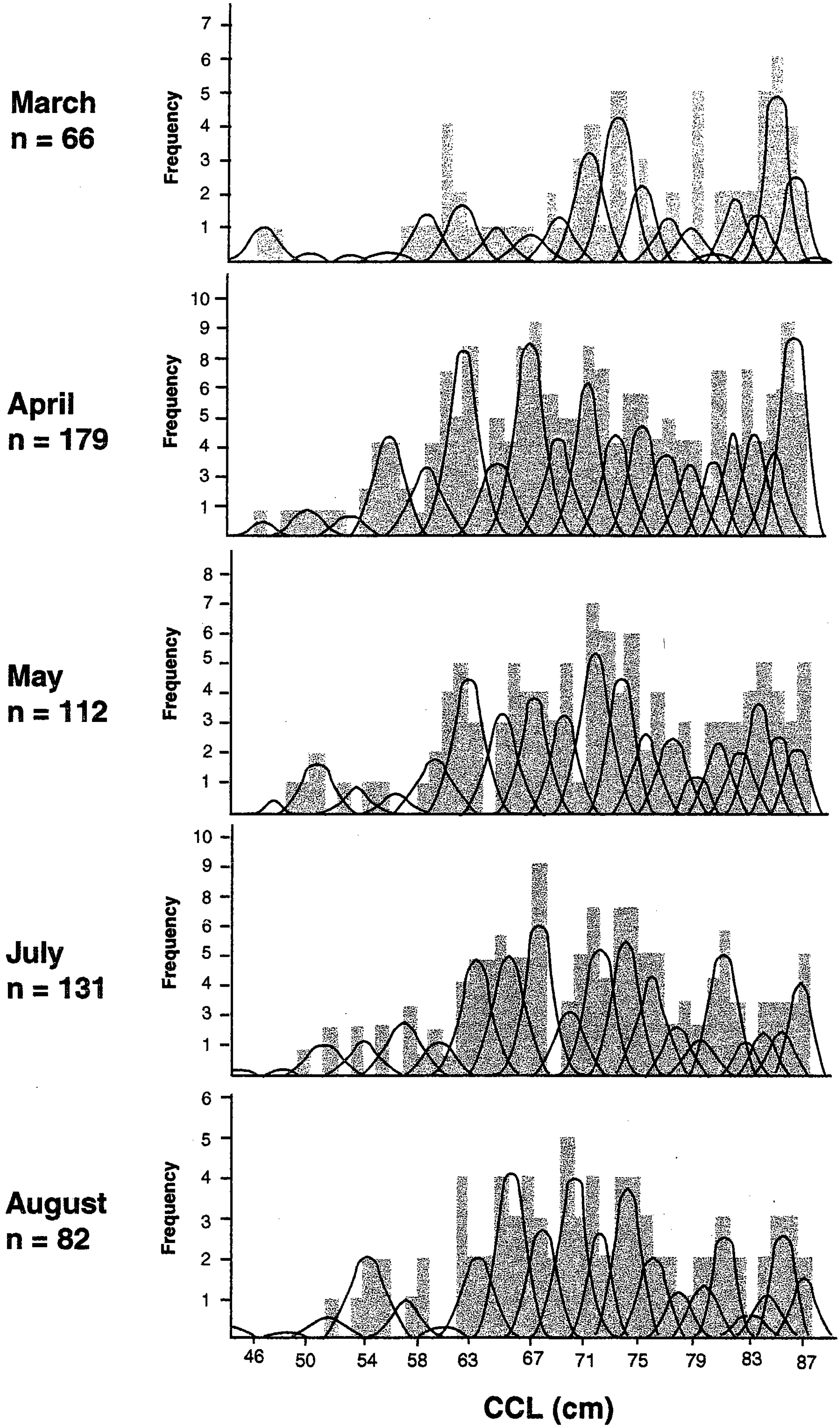


Figure 11. Von Bertalanffy growth model generated by MULTIFAN for loggerhead sea turtles stranded in the Gulf of Mexico from 1988 through 1995 within the size range of 46 to 87 cm curved carapace length. See text for equation.

Figure 12. Length-frequency distributions of combined-month samples for loggerhead sea turtles stranded in the Gulf of Mexico from 1988 through 1995 within the size range of 46 to 87 cm curved carapace length. Curves represent age-class modes assigned by MULTIFAN; midpoint of each mode indicates the mean CCL of each age class. Months not shown had samples that were too small to be representative of the population's length-frequency distribution, and thus were excluded from analyses.


March
n = 66
April
n = 179
May
n = 112
July
n = 131
August
n = 82
Frequency
46
50
54
58
63
67
71
75
79
83
87
CCL (cm)

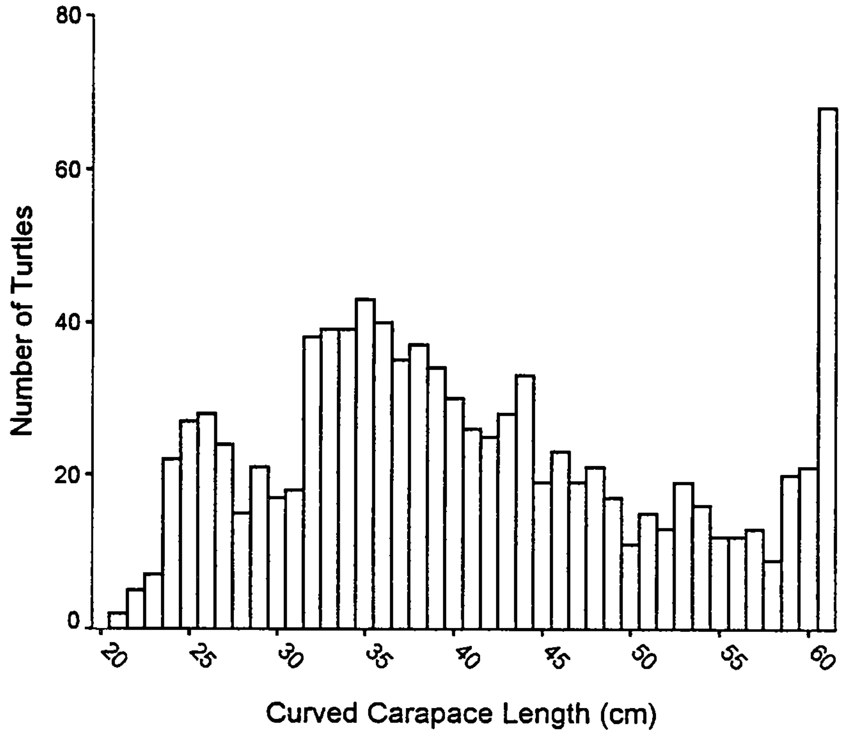


Figure 13. Size frequency of Kemp's ridleys stranded in the Gulf of Mexico from 1988 through 1995 within the size range of 20 to 61 cm curved carapace length.

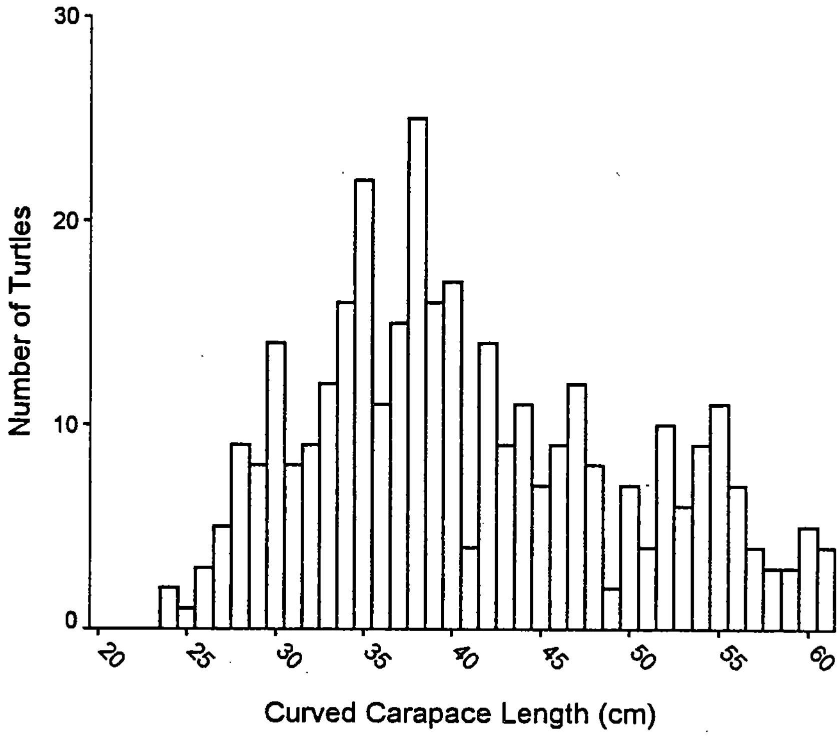


Figure 14. Size frequency of Kemp's ridleys stranded along the Atlantic coast of Florida and Georgia from 1988 through 1995 within the size range of 20 to 61 cm curved carapace length.

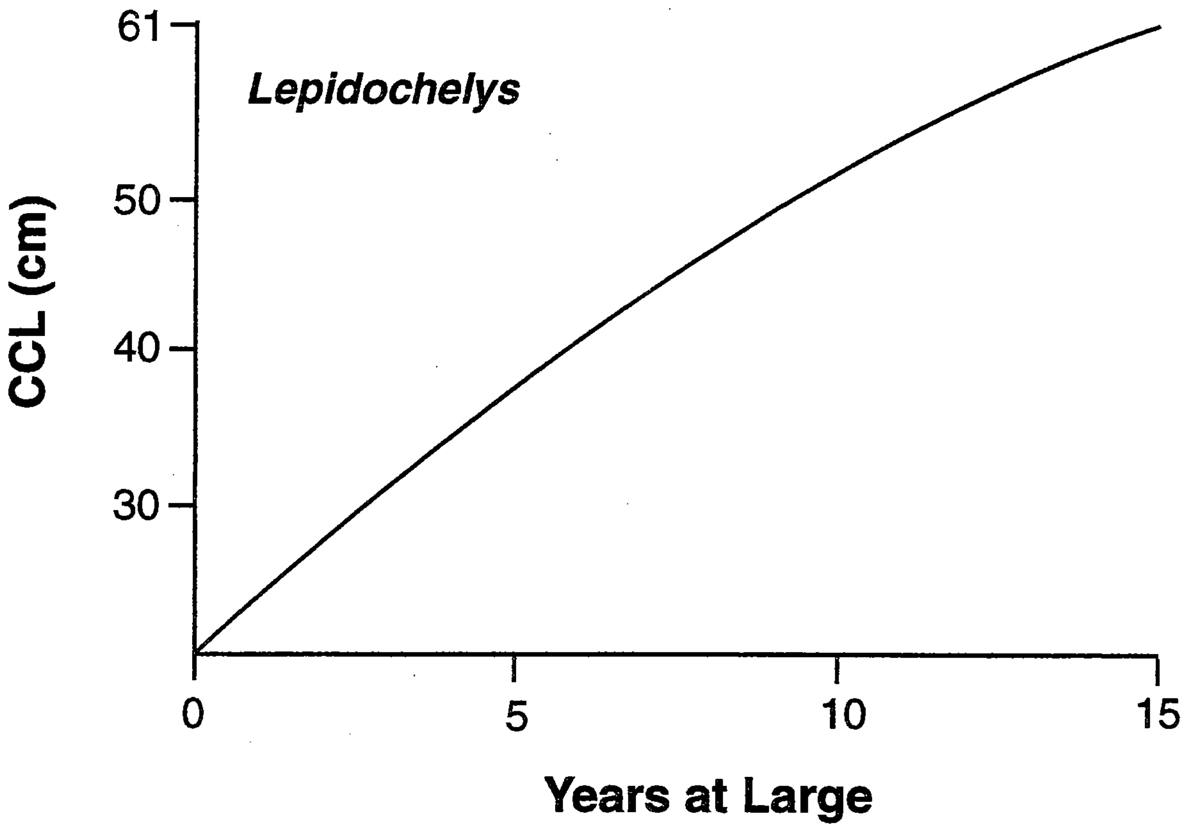
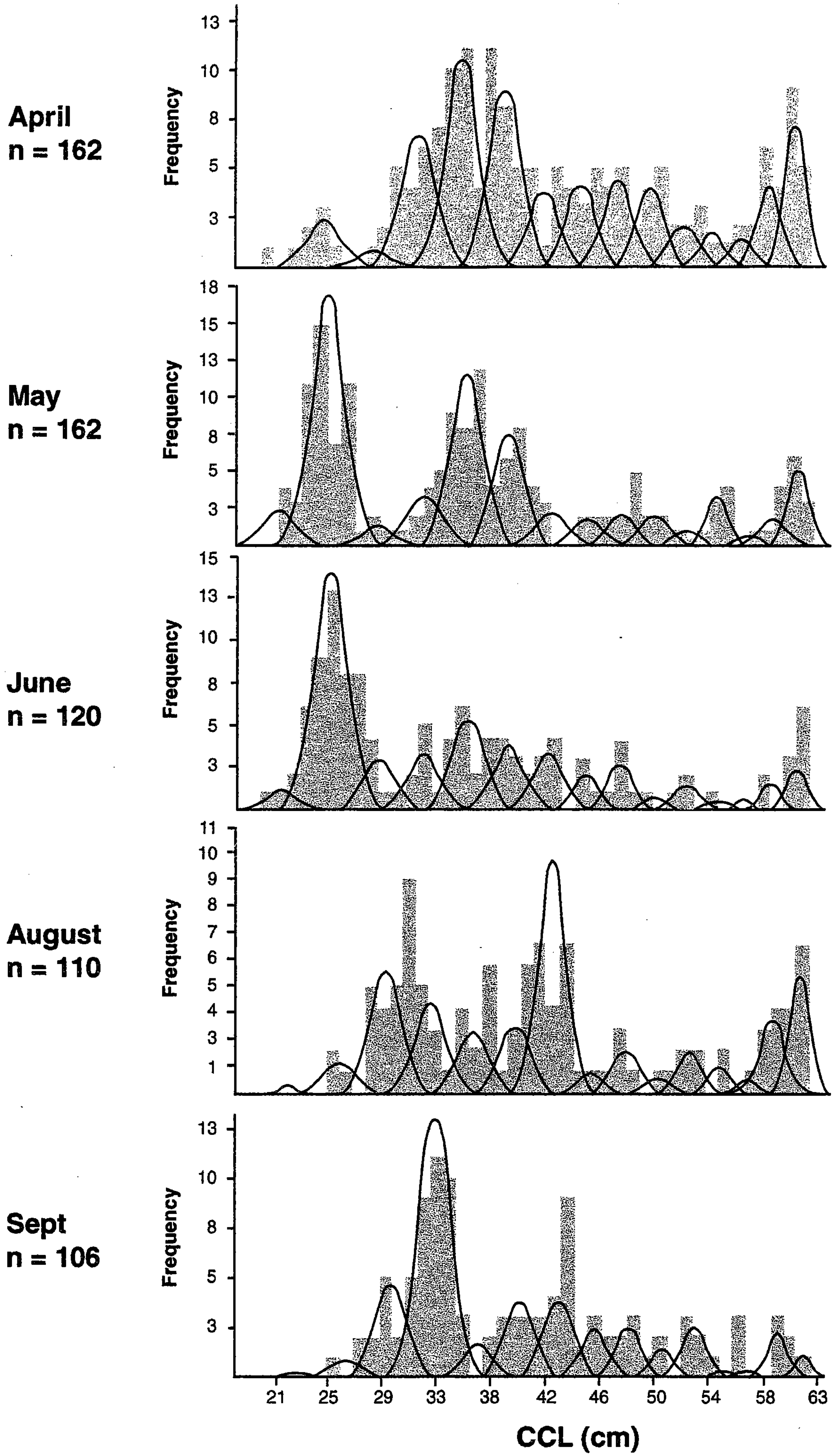


Figure 15. Von Bertalanffy growth model generated by MULTIFAN for Kemp's ridleys stranded in the Gulf of Mexico from 1988 through 1995 within the size range of 20 to 61 cm curved carapace length. See text for equation.

Figure 16. Length-frequency distributions of combined-month samples for Kemp's ridleys stranded in the Gulf of Mexico from 1988 through 1995 within the size range of 20 to 61 cm curved carapace length. Curves represent age-class modes assigned by MULTIFAN; midpoint of each mode indicates the mean CCL of each age class. Months not shown had samples that were too small to be representative of the population's length-frequency distribution, and thus were excluded from analyses.



April
n = 162
May
n = 162
June
n = 120
August
n = 110
Sept
n = 106
Frequency
21 25 29 33 38 42 46 50 54 58 63
CCL (cm)

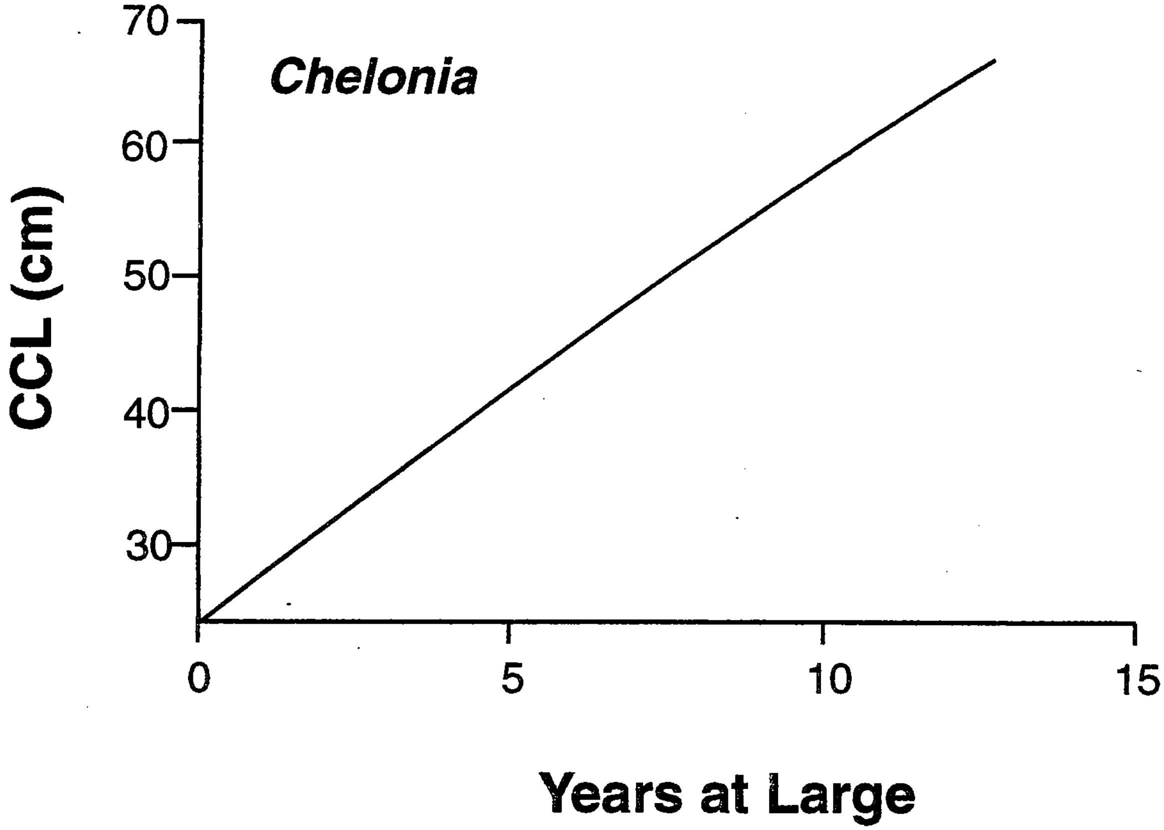
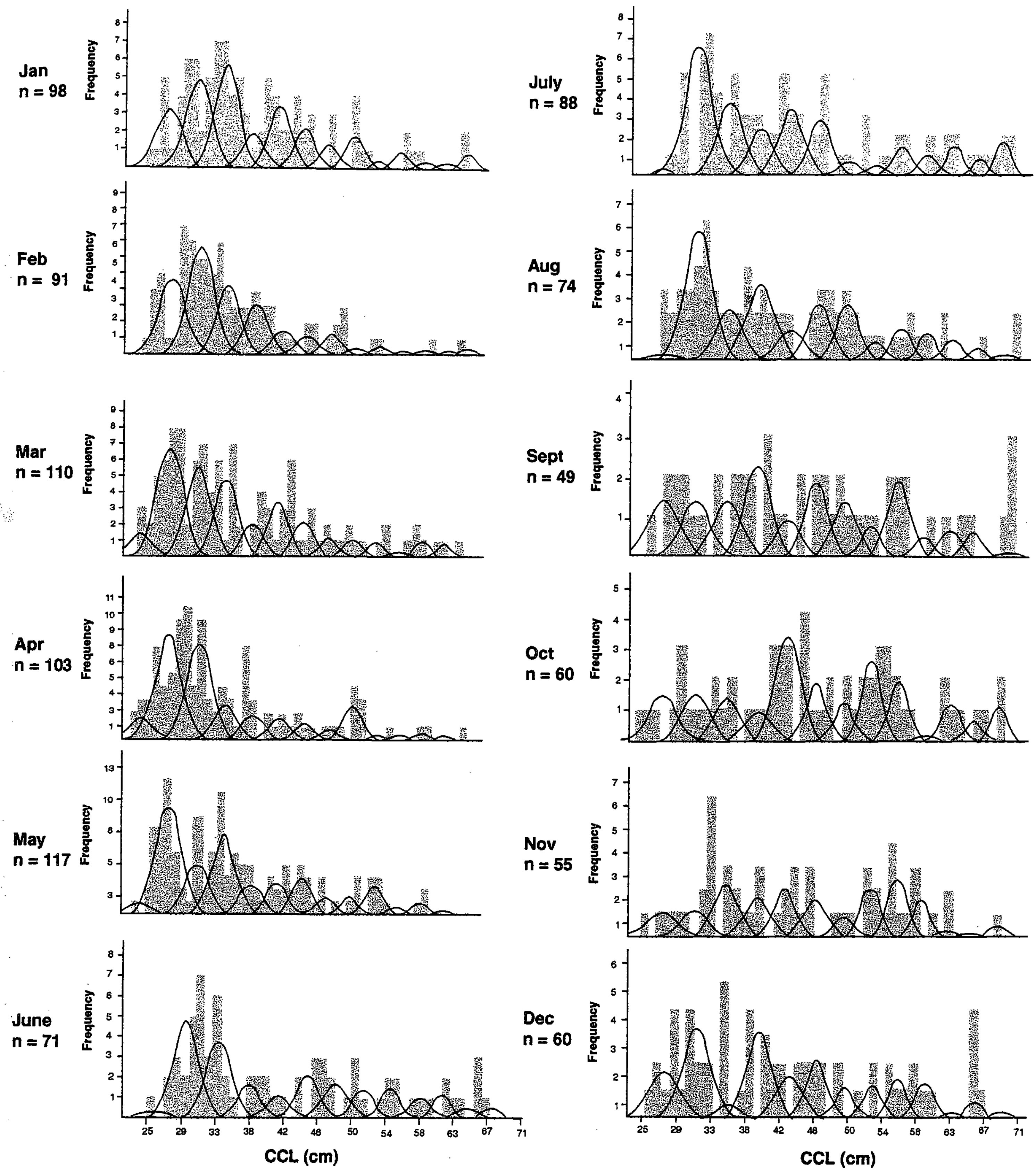


Figure 17. Von Bertalanffy growth model generated by MULTIFAN for green turtles stranded along the Atlantic coast of Florida from 1988 through 1995 within the size range of 25 to 70 cm curved carapace length. See text for equation.

Figure 18. Length-frequency distributions of combined-month samples for green turtles stranded along the Atlantic coast of Florida from 1988 through 1995 within the size range of 25 to 70 cm curved carapace length. Curves represent age-class modes assigned by MULTIFAN; midpoint of each mode indicates the mean CCL of each age class.


Jan
n = 98
Feb
n = 91
Mar
n = 110
Apr
n = 103
May
n = 117
June
n = 71
July
n = 88
Aug
n = 74
Sept
n = 49
Oct
n = 60
Nov
n = 55
Dec
n = 60
Frequency
25 29 33 38 42 46 50 54 58 63 67 71
CCL (cm)